UDC 575
DOI: 10.2298/GENSR1301273S
Review paper

THE *Drosophila ananassae* SPECIES COMPLEX: EVOLUTIONARY RELATIONSHIPS AMONG DIFFERENT MEMBERS

B.N. SINGH and Seema SISODIA

Genetics Laboratory, Department of Zoology, Banaras Hindu University,
Varanasi-221 005, INDIA,

Singh B.N., and S. Sisodia (2013): *The Drosophila ananassae species complex: evolutionary relationships among different members* Genetika, Vol 45, No. 1, 273-288.

Information about genetic structure and historical demography of natural populations is central to understanding how natural selection changes genomes. *Drosophila ananassae* is a widespread species occurring in geographically isolated or partially isolated populations and provides a unique opportunity to investigate population structure and molecular variation. *D. ananassae* and its closely related species serve as a widely used model in population and evolutionary genetics. The *ananassae* subgroup belongs to the *melanogaster* species group. This subgroup contains 22 described species distributed mainly throughout Southeast Asia, with some species expanding into northeastern Australia, South Pacific and Indian subcontinent and Africa. Within the *ananassae* subgroup, three species complexes-*ananassae, bipectinata and ercepeae* have been recognized based on male genital morphology. *D. ananassae* and its relatives have many advantages as a model of genetic differentiation and speciation. In this review, distribution, phylogenies, hybridization, sexual isolation among *D. ananassae* complex have been discussed. The complex of several cryptic island species provides a useful model for evolutionary studies dealing with the mechanisms of speciation.

Key words: Drosophila ananassae species complex; phylogenetic relationships; different members

INTRODUCTION

The fact that evolution is a continual and gradual process is perhaps nowhere better illustrated than in the genus *Drosophila*, where many detailed studies of reproductive isolation,

Corresponding author: B.N. Singh, Department of Zoology, Banaras Hindu University, Varanasi-221005, India. bnsingh@bhu.ac.in; bashisthsingh2004@rediffmail.com

chromosomal homologies and comparative morphology have demonstrated that, amongst the very large member of species in the genus, not a few exhibit an almost continuously variable range of phylogenetic divergence. In some cases, it is consequently very difficult although the species itself has been defined clearly enough (DOBZHANSKY, 1951, MAYR, 1963) to recognize distinct species within a complex of populations exhibiting partial or varying degrees of reproductive isolation from one another. Above the species level, correspondingly complicated taxonomic hierarchies have been developed in an attempt to group forms within the genus into successively higher level that reflects true evolutionary relationship (BOCK and WHEELER, 1972).

Drosophila melanogaster was described by MEIGEN in 1830 and is thus one of the oldest known members of the genus *Drosophila.* On the basis of comparative study of periphallic organs in the family Drosophilidae, HSU (1949) gave definition of many of the species groups of the genus *Drosophila* in terms of the detailed structure and setation of these organs. *D. melanogaste*r species group consists of 174 species (BOCK and WHEELER, 1972, LEMEUNIER *et al*. 1986, TODA, 1991). Twelve species subgroups have been described: *melanogaster, montium, ananassae, takahashii, suzukii, eugracilis, ficusphila, elegans, rhopaloa, denticulata, flavohirta,* and *longissima.* According to DA LAGE *et al*.(2007) sixty eight species or subspecies were studied: thirty from the *montium* subgroup, all nine known species in the *melanogaster* subgroup, seventeen from the *ananassae* subgroup and several species from the so-called 'Oriental subgroups'-*takahashii, suzukii, elegans, ficusphila, eugracilis* and additionally, *D. flavohirta.* All the reconstruction methods clearly show three main lineages with nested positions: (i) *melanogaster* + Oriental subgroup; (ii) *montium* subgroup; and (iii) *ananassae* subgroup.

The *ananassae* subgroup- pale to dark flies, male abdomen black in some species. Sex-comb in transverse row on the first two or three tarsal segments of male foreleg or one or two longitudinal or oblique metatarsal rows with one or a few additional teeth on the second tarsal segment (HSU, 1949).

The *ananassae* subgroup belongs to the *melanogaster* group, which includes 12 subgroups (TODA, 1991). The relationships among the different species groups are still not understood. ASHBURNER *et al*. (1984) made an attempt to integrate the chromosomal and morphological data to give an overall hypothesis of the relationships among the subgroups. They recognized three central lines within the *melanogaster* species group. *D. ananassae* subgroup constitutes the first of the central lines, the second consists of *montium* subgroup and the third is composed of the *suzukii*, *takahashii*, *ficusphila*, *melanogaster*, *elegans* and *eugracilis* subgroup. The remaining subgroups may be separated from these lines.

Two species complexes were recognized within the *ananassae* subgroup (BOCK, 1971, KANESHIRO and WHEELER, 1970, BOCK and WHEELER, 1972): the *ananassae* complex (aedeagus non-bifid, apically hirsute) and the *bipectinata* complex (aedegus bifid, bare, apically hooked). BOCK and WHEELER (1972) includes six species in *ananassae* complex and four species in *bipectinata* complex: *D.ananassae, D. pallidosa, D. phaeopleura, D. nesoetes, D. atripex* and *D. varians* are the members of the *ananassae* complex, *D. bipectinata, D. malerkotliana, D. parabipectinata* and *D. pseudoananassae* are the members of the *bipectinata* complex. *D. andamanensis* (GUPTA and RAY-CHAUDHURI, 1970) also belongs to the *ananassae* subgroup. Although, sex-comb of *andamanensis* is close to that of *bipectinata* and *parabipectinata*. In the absence of further information *andamanensis* is not assigned to either species complex. The affinities of *andamanensis* within the *ananassae* subgroup are not clear. The highly restricted geographic distribution of this species does however; resemble the situation in *pallidosa*, *nesotes*

and *phaeopleura* each species being known from one or a few small islands. The *ananassae* subgroup includes 22 species.

According to LEMEUNIER *et al*. (1986) the *ananassae* subgroup includes 18 species of which 2 species *malerkotliana* and *pseudoananassae* are polytypic. LEMEUNIER *et al*. (1986) included *ananassae, pallidosa phaeopleura nesoetes, atripex, varians, cornixa, lachaisei,* and *ironensis* total nine species in *ananassae* complex, four species in *bipectinata* complex (i.e. *bipectinata, malerkotliana, parabipectinata, pseudoananassae*). The other five species of the subgroup are not members of either species complex. Two of them, however, *D. ercepeae* and *D. vallismaia* are closely related (TSACAS, 1984). The biogeography of this species subgroup is very complex. It occupies a large area, from West Africa to Samoa. Two species *D. ananassae* and *D. malerkotliana* are very widespresd and sub cosmopolitan in their distribution. It is clear that it arose in South-East Asia, where nine species are endemic. The *ananassae* complex would appear to have radiated in the Pacific Islands. *D. atripex, D. varians* and *D. cornixa* are found in south-east Asia. The other being the endemic species. *D. pallidosa* (Fiji, Samoa). *D. phaeopleura* (Fiji), *D. nesoetes* (Palau), *D. ironensis* from Australia (Queensland) or *D. lachaisei* from West Africa. MC EVEY *et al*. (1987) described *D. monieri* sp. n. from French Polynesia. This new species breeds on rotting flowers of *Hibiscus titiaceus*. Now the *ananassae* complex includes 10 species.

D. ochrogater Chassagnard sp. n. 1992 of the *ananassae* subgroup is described and illustrated on specimens from New Caledonia. The New species is very close to *D. atripex* by its male genitalia and to *D. nesoetes.* It was confused with *D. atripex* in previous publication.

LEMEUNIER *et al*. (1997) introduced the *ercepeae* complex, a 3rd complex in the *ananassae* subgroup. They included four species. All species are insular endemic to Indian Ocean: *D. ercepeae*, Tsacas and David living in La Reunion, *D. vallismaia* Tsacas living in Seychelles, *D. merina* Tsacas sp.n. living in Madagascar and *D. comorensis* Tsacas sp.n. living in Comores. The *ercepeae* complex possesses all the characteristics of the *ananassae* subgroup, but differs from the two other complexes by the aedegus structure. It has a distinct basiphallus with two plates fused in their basal half and a distiphallus arising from these plates. The *ercepeae* complex constitutes the 3rd complex of the *ananassae* subgroup with regard to their external morphology, the four species are very similar but they may be distinguished by male genitalia. *D. varians* and *D. lachaisei,* which were once included in the *ananassae* complex (LEMEUNIER *et al*. 1986) are in fact found to be the most divergent species. *D. lachaise*i is always basal to the subgroup. The history of the *D. lachaisei* is very interesting which is considered to be of oriental origin (LEMEUNIER *et al*. 1986). *D. lachaisei* has been found as a rare species (a total of only some two dozen individuals have been caught) from western, central and eastern Africa. Interestingly, *D. lachaisei*, which is typically a palaeoendemic species with a broad fragmented and historical home range, is basal to the entire subgroup, suggesting a very ancient colonization of the Afrotropical region by a number of the *ananassae* group of which this species is probably relic (DA LAGE *et al*. 2007). MATSUDA *et al*. (2009) described a new species of *D. ananassae* species complex as *D. parapallidosa* Tobari sp.n. Twelve species have been described in the *D. ananassae* species complex but two of them were removed from this complex (DA LAGE *et al*. 2007); the complex now includes *D. ananassae, D. atripex, D. cornixa, D. ironensis, D. monieri, D. nesoetes, D. ochrogaster, D. pallidosa, D. parapallidosa, D. phaeopleura* (SAWAMURA *et al*. 2010).

MATSUDA *et al*. (2009) reported a number of strains whose species affiliations were unclear. These strains are similar to *D. ananassae* and *D. pallidosa*, but are partially reproductively isolated from these species and have distinct chromosome arrangements. Based on phenotypic traits, chromosome variation and reproductive isolation, they tentatively classified these strains into four taxa: *D. parapallidosa, D. pallidosa like, D. pallidosa like wau* and *D. papuensis-like*. They refer to the six species' including *D. ananassae, D. pallidosa* and four new taxa as the "*ananassae* species cluster", to distinguish it from the larger "*ananassae* species complex". The *ananassae* species complex is suitable for molecular phylogenetic and evolutionary studies because the entire genome of a strain of *D. ananassae* has been sequenced (*Drosophila* 12 Genomes Constorium 2007).

DISTRIBUTION

The centre of distribution of the *ananassae* subgroup is clearly in Southeast Asia. Both major lineages are represented in this region, with some species of the *ananassae* and the *bipectinata* species complexes extending into northeast Australia and the South Pacific. The main exception is the *ercepeae* complex, which is composed of insular endemics in the Indian Ocean where *D. ercepeae* occurs in La Reunion, *D. vallismaia* in the Seychelles, and *D. merina* in Madagascar and *D. lachaisei* is native to Africa.

The distribution of *ananassae* subgroup has been discussed by several authors (BOCK, 1980, TSACAS, 1984, LEMEUNIER *et al*. 1986, MC EVEY *et al*. 1987). TOBARI (1993) described the distribution of the 10 out of 11 species of the *ananassae* complex. LEMEUNIER *et al*. (1997) described the comparative distribution of the species of the three complexes of the *ananassae* subgroup. The *ananassae* subgroup occupies a large area from occidental Africa (west) to Touamutu Islands (east).They divided the area into five zones (LEMEUNIER *et al*. 1997, Fig 32)

Zone A- African continent, the most occidental area includes *D. lachaisei*, an endemic species is the only species belonging to the *ananassae* complex, it can be assumed that the introduction of *D. lachaisei* or its ancestor in occidental Africa happened during an ancient time by terrestrial introduction.

Zone B- includes the islands of the occidental part of the Indian Ocean including Madagascar. The 4 endemic species of the *ercepeae* complex are present together with one species (*D. bipectinata)* belonging to the widely distributed *bipectinata* complex. The *ananassae* complex is absent.

Zone C- includes the Indian subcontinent, Sri Lanka and the Andaman and Nicobar Islands. Only two widespread species (*D. bipectinata* and *D. pseudoananassae*) belonging to the *bipectinata* complex occur here. The *ananassae* complex is absent.

Zone D- includes Asia, Malaysia, Indonesia, the Philippines, New Guinea and Australia. It occupies the center of the distribution area of the subgroup. This area is also considered the origin area of the *melanogaster* group (BOCK and WHEELER, 1972) and may be even of the Drosophilidae itself (THROCKMORTON, 1975). Five endemic species of the *ananassae* complex are present (*D. atripex, D. cornixa, D. ironensis, D. nesoetes,* and *D. varians*) with 3 nonendemic species of the *bipectinata* complex, *D. bipectinata, D. parabipectinata and D. pseudoananassae.*. The great species diversity of this area might be explained by the existence of numerous islands that probably favored the radiation of the *ananassae* subgroup.

Zone E- corresponds to Oceania east to New Guinea and Australia. Four species of the *ananassae* complex (*D.monieri, D. ochrogaster, D. pallidosa* and *D. phaeopleura* are found with one non-endemic species of the *bipectinata* complex (*D. bipectinata*).

Among members of the *ananassae* species complex, *D. ananassae* is a cosmopolitan species but in contrast to *D. melanogaster* and *D. simulans*, populations throughout its geographical range are highly structured. A sibling species (*D. pallidosa*; BOCK and WHEELER, 1972) has been recorded in the Fijian Samoan Islands. The body colouration of *D. ananassae* is, furthermore, thought to be variable throughout its range (MC EVEY *et al*. 1987). It is the only cosmopolitan species of *Drosophila* that has been studied extensively by geneticists, has a completed genome sequence and exists in highly structured populations throughout its geographic range (reviewed in DAS *et al*. 2004, TOBARI, 1993). Like *D. melanogaster* and *D. simulans, D. ananassae* is found most frequently in association with humans and outside Southeast Asia rarely in natural habitats (BOCK and PARSONS, 1978).

PHYLOGENY

Comparative genetic and molecular research in *D. ananassae* and its relatives will require a phylogenetic framework. Historical information is essential for reconstituting the evolution of behaviour and other phenotypic traits, understanding the demographic history of each species and inferring the evolutionary forces acting on molecular sequence. *D. ananassae* and its relatives have many advantages as a model of genetic differentiation and speciation. DA LAGE *et al*. (2007) used *Amyrel* gene sequences to confirm the monophyly of each species complex and resolve phylogenetic relationship within and among these complexes. In other *Drosophila* lineages, however different loci often support different species relationships (KOPP and TRUE, 2002, POLLARD *et al*. 2006, WONG *et al*. 2007) suggesting that additional sequence data may provide valuable historical information.

MATSUDA *et al*. (2009) studied phylogentic relationships in the *ananassae* species subgroup. Phylogenetic analysis reveals two major lineages within the *ananassae* subgroup. The first lineage is composed of the *ananassae* and *bipectinata* species complex, and the other of *ercepeae* complex and *D. varians*. *D. varians* has sometimes been grouped with the *ananassae* complex based on the morphology of male genitalia (BOCK and WHEELER, 1972). The new molecular phylogenies suggest that morphological similarities may reflect convergent evolution.

The *ercepeae* complex is monophyletic in all single-locus analyses, and the *bipectinata* complex is monophyletic in all gene trees except *Gpdh*. *D. monieri, D. phaeopleura, D. ochrogaster* and *D. atripex* tend to be grouped with *D. ananassae* and its close relatives *D parapallidosa* in most trees. Finally, *D. varians* is usually close to *ercepeae* complex. MATSUDA *et al*. (2009) presented two major clades emerge in the multilocus phylogeny. The first consists of the *ercepeae* species complex and *D. varians* while the second includes the *ananassae* and *bipectinata* species complex. In the *ananassae* complex, three South Pacific species (*D. phaeopleura, D. monieri* and *D. ochrogaster*) cluster with the Southeast Asian *D. atripex*, with *D. ananassae* and *D. parapallidosa* forming the other monophylectic branch within this complex.

MATSUDA *et al*. (2009) described morphological evolution in the *ananassae* subgroup. Most species in the *ananassae* subgroup have “transverse” sex combs composed of several rows of thickened bristles oriented perpendicular to the proximo-distal leg axis. However, *D. bipectinata* and *D. parabipectinata* in the *bipectinata* complex have rotated sex combs which

develop from the same precursor bristles as the transverse sex combs of other species, but are arranged along the proximo-distal leg axis and are curved and highly melanised (KOPP and BARMINA, 2005). This morphology makes these two species drastically different from all other members of the *ananassae* subgroup, but is remarkably similar to the sex combs of several more distantly related species.

D. ananassae, D atripex, D. bipectinata, D. vallismaia and *D. varians* which together represent all major lineage in the *ananassae* subgroup, have similar karyotypes consisting of medium sized metacentric X, two large metacentric autosomes, and medium or large metacentric 4^{th} chromosomes. Males also carry a submetacentric or metacentric Y chromosome. In the meiotic nuclei of primary spermatocytes, a tetravalent between X, Y and 4^{th} chromosomes is observed in all species of the *ananassae* subgroup except the three members of *ercepeae* complex (*D. merina, D. vallismaia* and *D. ercepeae)*(MATSUDA *et al*. 2009).

In the *ananassae* subgroup, only the species belonging to the *ercepeae* complex were found to carry nucleous organizer (NORs) on both the sex chromosomes, which is the general pattern in the *melanogaster* subgroup. This pattern is ancestral in *melanogaster* group, and that *ercepeae* complex was the first to evolve within the subgroup. The loss of the Y- and X- linked NORs and the acquisition of an NOR on the fourth chromosome would seem to have occurred in the lineage leading to the *ananassae* and *bipectinata* complex before they split. According to ROY *et al*. (2005) the presence of a Y-linked NOR in *D. ananassae* results from a secondary acquisition. The absence of a Y-linked NOR in *D. pallidosa*, which is thought to be its closest relative (SINGH 2000) support this hypothesis. This would imply that the NOR on the fourth chromosome, as proposed by HINTON and DOWNS (1975), but may have originated from the Y-chromosome.

SAWAMURA *et al*. (2010) explained evolutionary relationships in the *Drosophila ananassae* species cluster based on the introns of multiple nuclear loci. They examined DNA sequences of introns in four loci: alpha actinin (*Actn*) on XL, white (w) on X, CG7785 on 2L and zincion transmembrane transporter 63C (ZnT63C) on 2R. Phylogenetic trees (neighbor-joining and haplotype network) were inconsistent among these loci. Some haplotypes shared between taxa were found for w, CG7785 and ZnT636 suggesting recent gene flow. However, no haplotypes were shared, for example, between *D. ananassae* and *D. pallidosa* for CG7785, which is close to the proximal breakpoints of In (2L) D. This suggests that taxon-specific inversions prevent gene flow, as predicted by the chromosomal speciation hypothesis.

D. varians possesses sex chromosomes and a chromosome 4, which have heterochromatic banding patterns very different from those of the species belonging to the three complexes. *D. varians* has a unique NOR, situated on the shorter arm of the submetacentric chromosome 4 close to the centromere.

The phylogenetic position of *D. varians* is still unclear. Its inclusion in the *ananassae* subgroup was initially challenged, on the basis of some characteristics of its periphallic organs (BOCK and WHEELER, 1972). Recent molecular data support this assignation, but do not enlighten us about the relationship of this species with the three complexes (SCHAWAROCH, 2002). The structure of mitotic chromosomes does not provide any further information about its possible position within the subgroup. However, the presence of an NOR on its fourth chromosome tends to bring *D. varians* closer to the *bipectinata* and *ananassae* complexes.

HYBRIDIZATION

Understanding the mechanisms of speciation is one of the prime targets for evolutionary biologists. *D. ananassae* and *D. pallidosa* are very closely related species that can produce viable and fertile hybrids of both sexes, although strong sexual isolation exists between the two species. *D. ananassae* is a cosmopolitan and circumtropical species, but *D. pallidosa* is endemic to islands of the South Pacific Ocean. In spite of their sympatric distribution, post mating reproductive barriers such as hybrid sterility or hybrid inviability does not exist between them (BOCK and WHEELER, 1972, FUTCH, 1966). Female sex pheromones (NEMOTO *et al*. 1994, DOI *et al*. 1997) and male courtship songs (YAMADA *et al*. 2002a,b) differ between the species and are thought to be used by them for species recognition. DOI *et al*. (2001) and YAMADA *et al*. (2002a) surgically removed male wings or female antennae, the emitter and receiver organs of acoustic signals respectively, and examined the mating success of intraspecific and interspecific crosses. The mating success decreased in intraspecific crosses but dramatically increased in interspecific crosses. Because many of the genetic markers are known (MORIWAKI and TOBARI, 1993) and the entire genomic DNA has been sequenced recently in *D. ananassae* (GIBERT, 2007), the *ananassae* and *pallidosa* species pair seems suitable for genetic and molecular analyses of sexual isolation. DOI *et al*. (2001) mapped genes contributing to the female discrimination behaviour by different methods and concluded that a gene or genes closely linked to Delta (Dl) are responsible for the behaviour leading to sexual isolation. SAWAMURA *et al*. (2008a) analysed genetic basis of female discrimination behaviour by using isogenic females from interspecific mosaic genome lines that carry homozygous recombinant chromosomes. Multiple regression analysis indicated a highly significant effect of left arm of chromosome 2 (2L) on the willingness of females to mate with *D. ananassae* males. Not only 2L but also the left arm of chromosome X (XL) and the right arm of chromosome 3 (3R) had significant effects on the female's willingness to mate with *D. pallidosa* males. All regions with strong effects on male choice have chromosome arrangements characterized by species-specific inversions. Heterospecific combinations of 2L and 3R have previously been suggested to cause postzygotic reproductive isolation. Thus, genes involved in premating as well as postmating isolation are located in or near chromosomal inversions. VISHALAKSHI and SINGH (2006) tested sexual isolation between *D. ananassae* and *D. pallidosa*. From the results of their study, it is concluded that there is strong ethological isolation between *D. ananassae* and *D. pallidosa* which is not affected by different experimental conditions.

D. ananassae and *D. pallidosa* may have several cryptic species, which together we refer to as the *D. ananassae* species cluster. The cryptic species are different in the chromosome constitution (i.e. carrying at most eleven specific inversions) and courtship songs (FUTCH, 1966, TOMIMURA *et al*. 1993, YAMADA *et al*. 2002) despite their morphological similarity, they can be distinguished by reproductive isolation (DOI, 1997, SCHUG *et al*, 2008) among the potential cryptic species of the *D. ananassae* species cluster, one inhabiting Papua New Guinea, called *pallidosa-like*; is phenotypically similar to *D. pallidosa* and shares with it all chromosomal inversions except one or two (TOBARI, 1993, TOMIMURA *et al*. 1993). Because *pallidosa-like* populations exhibit phenotypic variation and are sometimes intermediate between *D. ananassae* and *D. pallidosa*, these populations may be of hybrid origin or represent a hybrid swarm, some of the *pallidosa-like* flies first collected in Wau, Papua New Guinea are apparently reproductively isolated from the others and this population is called *pallidosa–like Wau*. FUTCH(1966) recognized another cryptic species in Papua New Guinea, and this population is called *papuensis*. Similar flies (*papuensis-like*) were collected in later expedition but the

chromosome configuration is slightly different (TOMIMURA *et al*. 1993). This may have been caused by recent introgression from *D. ananassae*. *D. papuensis like* also has been recorded in Cairns, Australia (TOBARI, 1993). Another cryptic species, Taxon- K has been found in Kota Kinabalu, Borneo, Malaysia (TOBARI 1993; TOMIMURA et al. 1993). Its distribution has been expanding in Southeast Asia, and the flies can now be collected in Taiwan and Yaeyana Islands in Japan. SAWAMURA *et al*. (2008b) reported that a pseudogene with 94% similarity to mitochondrial cytochrome C oxidase subunit I (COI) was identified and localized to cytochrome 4 of *D. ananassae*. Because this chromosome is believed to have reduced recombination, its history can be traced using the pseudo-COI sequence, pseudo-COI sequence were obtained from 27 iso-female lines of six taxa belonging to the *D. ananassae* species cluster in which reproductive isolation is incomplete. The phylogenetic network constructed from seven recognized haplotypes indicated that different taxa inhabiting the same geographic area share the haplotypes. They also reported a potential gene flow in natural populations of the species cluster inferred from a nuclear mitochondrial pseudogene. To understand geographic differentiation of populations of *D. ananassae* and the relationship of the latter to *D. pallidosa*, microsatellites and mitochondrial DNA have been investigated, which led to the realization that *D. ananassae* is a polytypic species even in the same locality (SCHUG *et al*. 2004, 2007, 2008). SAWAMURA (2008b) and MATSUDA *et al*. (2009) analyzed genes from chromosome 4, chromosome Y and the mitochondrial genome to understand relationships in the *D. ananassae* species cluster, but the phylogenetic resolution was too low to resolve the relationship, presumably because of introgression and/ or lineage sorting.

ROY *et al*. (2005) investigated the evolution of chromosomal location of ribosomal RNA gene clusters and the organization of heterochromatin in the *D. melanogaster* group by using fluorescence in situ hybridization and DAPI staining to mitotic chromosomes. In this study, the four species of *D. ananassae* complex studied are devoid of nucleous organizer (NORs) on the X chromosomes and *D. ananassae* is only to display a NOR on the Y chromosomes. All have an NOR on the metacentric (or submetacentric) chromosome 4. In *D. ananassae* and *D. phaeopleura*, the hybridization site is terminal, whereas in *D. atripex* and *D. pallidosa* the site appears to be closer to the centromere. In *D. atripex* and *D. phaeopleura* differences were observed in the size of the rhodamine signals between the homologues of chromosome 4. The differences are strongly marked in *D. phaeopleura*, for which the largest rhodamine signal is associated with additional heterochromatic material.

PARTHENOGENESIS

Parthenogenesis in animals is a well-known phenomenon. The first attempt to demonstrate the genetic basis of parthenogenesis in *Drosophila* was carried out by STALKER (1951, 1954). The mechanism of parthenogenesis in diploid females is known to be automictic via a variety of post-meiotic nuclear fusion events that produce diploid progeny. Parthenogenetic strains of several species have been found in the genus *Drosophila*. The mode of diploidization in the eggs of females has been found to be post-meiotic nuclear fusion. The genetic basis for this parthenogenesis is not understood but is believed to be under the control of a complex polygenic system. FUTCH (1972) found that the parthenogenetic females were rare in collection. He made a systematic examination for parthenogenesis in many geographical stocks from Mexico, Hawaii, Palmyra Island, Marshall Islands, Fiji, Cook Islands and Papua New Guinea populations and found that only females of *D. pallidosa* from the Western Samoa, American

Samoa and Tonga population and *D. ananassae* from the Western Samoa and American Samoa population, had parthenogenetic capacity In the Samoan Islands, populations of two species, *D. ananassae* and *D. pallidosa* have kept the *parth* gene. This may suggest that occurrence of some gene flow between them, as FUTCH (1972, 1973) suspected. *D. pallidosa-like* collected from Lae, Papua New Guinea are morphologically indistinguishable from *D. pallidosa,* and carry the *'D. pallidosa* chromosome', but are ethologically isolated (TOMIMURA *et al*. 1993). This may indicate that the *parth* gene has been derived from their ancestral species and kept in their populations during the course of speciation.

Parthenogenetic strains of *D. ananassae* and *D. pallidosa* collected in Taputimu, American Samoa were established by FUTCH (1972). MATSUDA and TOBARI (1999) found that more than 80% of females from parthenogenetic strains produced progeny parthenogenetically and that inter-specific hybrid females also produced impaternate progeny. They also reported that the mode of parthenogensis of *D. ananassae* appears to be the post-meiotic nuclear folding of a single meiotic product, and that a major gene responsible for the parthenogenesis maps to the left are of the second chromosome of *D. ananassae*. The genetic basis for parthenogenetic capacity may be identical among the three closely related species.

SEXUAL ISOLATION

Sexual isolation before fertilization may be one of the most important isolating mechanisms leading to speciation. Prezygotic mating isolation has been a major interest of evolutionary biologists during the past several decades because it is likely to represent one of the first stages in the transition from populations to species. Male discrimination is one of the most commonly measured forms of prezygotic isolation and appears to be relatively common among closely related species. SCHUG *et al*. (2008) measured the level and pattern of mate discrimination among 18 populations of a cosmopolitan Drosophilid species *D. ananassae* from throughout its geographical range and its sister species, *D. pallidosa* which has a restricted geographical distribution in the South Pacific Island. Mate discrimination varies being higher among populations outside the ancestral Indonesian range, and highest in the South Pacific. They also reported that colonization and genetic differentiation may have an influence on the evolutionary origin of mate discrimination.

Genes with sex-biased expression often show rapid molecular evolution between species. Previous population, genetic and comparative genomic studies of *D. melanogaster* and *D. simulans* revealed that male-biased genes have especially high rates of adaptive evolution. To test if this is also the case for other lineage within the *melanogaster* group, GRATH *et al*. (2009) investigated gene expression in *D. ananassae*, a species that occurs in structural populations in tropical and subtropical regions. Sex-biased expression is generally conserved between *D. melanogaster* and *D. ananassae* with the majority of genes exhibiting the same bias in two species. For analysis of evolutionary rates and tests for adaptive evolution, it is critical to have an appropriate outgroup species. Two recent molecular phylogenetic studies suggested that *D. atripex* and *D. phaeopleura* might serve as an appropriate outgroup to *D. ananassae* for those purposes. To further investigate the phylogenetic relationship of these, the amino acid sequence was used to generate phylogenetic tree. The tree topology was strongly supported and indicated that *D. atripex* and *D. phaeopleura* are more closely related to each other than is to *D. ananassae*. Thus both of these species can be used as an outgroup to *D. ananassae*. Furthermore, the divergence between *D. ananassae* and *D. atripex*/*D. phaeopleura* is similar to the divergence

between *D. melanogaster* and *D. simulans*, which facilitates that comparison of evolutionary patterns between the *melanogaster* and *ananassae* subgroup. For a long time, *D. ananassae* and *D. pallidosa* were thought to be one species comprised of light and dark forms, even though they were cytologically and ethologically distinguished (FUTCH, 1966, SPIETH, 1966, STONE *et al*. 1966). BOCK and WHEELER (1972) recognized the two as distinct species, with the dark identified as *D. ananassae*, and the light as *D. pallidosa*. The major morphological differences between the two species are the body colour and the number of rows in the sex comb. These similarities suggest that phylogenetic separation of *D. ananassae* and *D. pallidosa* must have been one of the more recent events of speciation in the *melanogaster* group. *D. ananassae* and *D. pallidosa* do not exhibit postmating isolation such as hybrid inviability and sterility (FUTCH, 1966, STONE, 1966). This indicates that only sexual (ethological isolation can prevent gene flow between these two (FUTCH, 1966, 1973, SPIETH, 1966). DOI *et al*. (1997) studied behavioural response of males to major sex pheromone component (Z, Z-5, 25-hentriaccontadiene of *D. ananassae* females. Cuticular hydrocarbon differences between *D. ananassae* and *D. pallidosa* were noteworthy with respect to C31 and C33 carbons: *D. ananassae* predominantly possesses the former (63% of total cuticular hydrocarbon) and *D. pallidosa* the latter (57%). However, except for the C31 and C 33 carbons both species had almost the same ratio of the other cuticular hydrocarbons. Furthermore, since neither qualitative nor quantitative difference between males and females were observed in either species (NEMOTO *et al*. 1994). The only significant difference in cuticular hydrocarbon composition between *D. ananassae* and *D. pallidosa* is the difference in major pheromone compounds. Differences in cuticular hydrocarbons contribute to sexual isolation between close relatives (COYNE *et al*. 1994; COYNE and OYAMA, 1995). Sexual isolation maintained by strong mating preference has been reported in the light and dark forms of *D. ananassae* in laboratory stocks (FUTCH, 1966). These forms were found to be sibling species (*D. ananassae* and. *pallidosa*) of the *ananassae* complex which show strong sexual isolation (FUTCH, 1973, DOI *et al*. 2001, SAWAMURA *et al*. 2006, VISHALAKSHI and SINGH, 2006). *D. ananassae* and *D. pallidosa* lack postmating isolation. Sexual isolation has been considered important in maintaining them as independent species. Courtship songs appear to be of crucial importance in the sexual isolation of *D. ananassae* and *D. pallidosa*. Behavioural isolation has been found between two karyotypically different homozygous strains of *D. ananassae* derived from same geographic location which shows that chromosome arrangements may affect mate recognition system in *D. ananassae*. Sexual isolation may originate due to founder effects in *D. ananassae.* These findings suggest that there is instability of mate recognition system in *D. ananassae* (NANDA and SINGH, 2011a,b). YAMADA *et al*. (2008) examined male and female sexual behaviours of *D. ananassae* and *D. pallidosa* to clarify the process that leads to strong sexual isolation between these sympatric species. Results revealed that sexual isolation between *D. ananassae* and *D. pallidosa* is a function of the following behavioural sequence: courtship start ⟶ male wing vibration ⟶ female wing fluttering⟶ male courtship discontinuation.

PREMATING REPRODUCTIVE ISOLATION IN *ANANASSAE* CLUSTER

MATSUDA *et al*. (2009) reported pre-mating reproductive isolation in the *ananassae* species cluster. *D. pallidosa-like wau* shows strong pre-mating reproductive isolation in the *ananassae* species cluster. *D. pallidosa-like wau* shows strong pre-mating isolation from the other five taxa, except the cross between *D. parapallidosa* females and *D. pallidosa wau* males. *D. papuensis-like* shows strong isolation from *D. parapallidosa, D. pallidosa*-like and *D.*

pallidosa like wau but more moderate isolation from *D. ananassae* and *D. pallidosa. D. pallidosa* – like is strongly isolated from *D. pallidosa-like* wau, D. *papensis*-like and *D. ananassae*, but shows much weaker isolation from *D. pallidosa* and *D. parapallidosa*, consistent with previous reports (FUTCH, 1966, DOI *et al*. 2001). MATSUDA *et al*. (2009) also observed strong premating isolation in crosses between *D. pallidosa* males and *D. ananassae* females, but not in the reciprocal crosses. *D. ananassae* shows a similar asymmetric isolation from *D. parapallidosa*. In contrast, *D. pallidosa* shows only mild pre-mating isolation from the *D. parapallidosa* in either direction. In general, differences in insemination success between reciprocal crosses are common in the *ananassae* species cluster.

Post zygotic reproductive isolation: MATSUDA *et al*. (2009) examined F_1 hybrid male sterility in all pair wise crosses among the six taxa of the *ananassae* species cluster. No progeny were produced in crosses between *D. papuensis* like males and either *D. pallidosa –like* or *D. pallidosa-like wau* females despite repeated attempts to cross different strains. This strongly provides evidence for pre-mating isolation between these taxa. In remaining 28 species pairs, fertile F_1 hybrid males were produced in 16 combinations, four species pairs produced only sterile males in all crosses, and the eight pairs yielded either fertile or sterile F_1 males when different parental strains were used. When *D. ananassae* and *D. pallidosa* are used as male parent, fertile male hybrids are used. In contrast, sterile hybrid males were found almost exclusively in crosses involving *D. parapallidosa*, *D. pallidosa like wau* or *D. pallidosa-like* as the male parent. *D. parapallidosa* shows particularly strong isolation from the other species.

D. ananassae is a widespread species occurring in geographically isolated or partially isolated populations and to provides a unique opportunity to investigate population structure and molecular variation. Numerous studies in *D. ananassae* have focused on genetic differentiation, inversion polymorphism, sexual behaviour and reproductive isolation (SCHUG *et al*. 2007, MATSUDA and TOBARI, 2004, YAMADA *et al*. 2002, DOI *et al*. 2001, DAS *et al*. 2004, for references see SINGH, 2010). *D. ananassae* shows high degree of chromosomal variability. In total, there are seventy eight paracentric, twenty one pericentric inversions and forty eight translocations reported so far in this species (SINGH and SINGH, 2007). Population genetics of three cosmopolitan inversions AL, DL and ET have been extensively studied by SINGH and his students (SINGH, 1996, 2010, SINGH and SINGH, 2008). Further, Indian *D. ananassae* populations also show effect of different geographical parameters (latitude, altitude and longitude) and climatic variables (average annual temperature, average annual rainfall and relative humidity) on multiple traits: desiccation, starvation, lipid content, heat resistance and chill-coma recovery (SISODIA and SINGH, 2010 a,b).

CONCLUSION

Drosophila ananassae and its relatives have many advantages as a model of studies on genetic differentiation and speciation. The *D. ananassae* species complex is suitable for molecular phylogenetic and evolutionary studies because the entire genome of a strain of *D. anananssae* has been recently sequenced. In fact the population structure and its sibling species has been analyzed using several nuclear/mitochondrial genes and microsatellites. The recent sequencing of *D. ananassae* genome and the availability of whole genome microarrays (CLARK *et al*. 2007, ZHANG *et al*. 2007) will further enhance the power and the utility of this model. In particular

genomic approaches may help identify the molecular-genetic and neurophysiological changes responsible for the evolution of mating behaviour and sexual isolation in *D. ananassae*.

ACKNOWLEDGEMENT

Financial assistance in the form of Women Scientist Scheme from the Department of Science and Technology, New Delhi to SS is gratefully acknowledged.

Received Juny21h, 2012
Accepted April 08th, 2013

REFERENCES

ASHBURNER, M., M. BODMER., F. LEMEUNIER (1984): On the evolutionary relationships of *Drosophila melanogaster*. Dev. Genet. *4*, 295-312.

BOCK, I.R. (1971): Taxonamy of the *Drosophila bipectinata* species complex. Univ. Texas Publ. *7103*, 273-280.

BOCK, I.R (1980): Current status of the *Drosophila melanogaster* species group (Diptera). Syst. Entomol .*5*, 341-356.

BOCK, I.R. and P.A.PARSON (1978): Australian endemic *Drosophila* IV Queensland rainforest species collected at fruit baits, with description of two species. Aust. J. Zool. *26*, 91-103.

BOCK, I.R. and M.R. WHEELER (1972): The *Drosophila melanogaster* species group. Univ. Texas Publ. *7213*, 1-102.

CLARK, A.G., M.B. EISEN, D.R. SMITH, C.M. BERGMAN, B. OLIVER, *et al*. (2007): Evolution of genes and genomes on the *Drosophila* phylogeny. Nature *450*, 203-218.

COYNE, J.A. and R. OYAMA (1995): Localization of pheromonal sexual dimorphism in *Drosophila melanogaster* and its effect on sexual isolation. Proceedings of the National Academy of Sciences USA 92, 9505–9509.

COYNE, J.A., A.P. CRITTENDEN, K. MAH (1994): Genetics of a pheromonal difference contributing to reproductive isolation in *Drosophila*. Science 265, 1461–1464.

DA LAGE, J.L., G.J. KERGOAT, F. MACZKOWIAK, J.F. SILVAIN, M.L. CARIOU, D. LACHAISE (2007): A phylogeny of Drosophilidae using the *Amyrel* gene: questioning the *Drosophila melanogaster* species group boundaries. J. Zool. Syst. Evol. Res. *45*, 47-63.

DAS, A., S. MOHANTY, W. STEPHAN (2004): Inferring the population structure and demography of *Drosophila ananassae* from multilocus data. Genetics *168*, 1975-1985.

DOBZHANSKY, TH. (1951): Genetics and the origin of species. Columbia Univ. Press, New York.

DOI, M., M. MATSUDA, M.TOMARU, H. MATSUBAYASHI, Y.OGUMA (2001): A locus for female discrimination behaviour causing sexual isolation in *Drosophila*. Proc. Natl. Acad. Sci. U.S.A. *98*, 6714-6719.

DOI, M., T. NEMOTO, H. NAKANISHI, Y. KUWAHARA, Y. OGUMA (1997): Behavioural response of males to females. J. Chem. Biol. *23*, 2067-2078.

FUTCH, D.G. (1966): A study of speciation in South Pacific populations of *Drosophila ananassae*. Univ. Texas Publ. *7215*, 79-120.

FUTCH, D.G. (1972): A preliminary note on parthenogenesis in *Drosophila ananassae*. Dros. Inf. Serv. 48, 78.

FUTCH, D.G. (1973): On the ethological differentiation of *Drosophila ananassae* and *D. pallidosa*. Evolution *27*, 456-467.

GILBERT, D.G. (2007): DroSpeGe: rapid access database for new *Drosophila* species genomes. Nucl. Acids Res. 35, D480-D485.

GRATH, S., J.F. BAINES, J. PARSH (2009): Molecular evolution of sex-biased genes in the *Drosophila ananassae* subgroup. BMC Evol. Biol. *9*, 291-300.

GUPTA, J.P. and S.P. RAY-CHAUDHURI (1970): The genus *Drosophila* (Diptera: Drosophilidae) in Andaman and Nicobar Islands, India. Orient Insects *4*, 169-175.

HINTON, C.W. and J.E. DOWNS (1975): The mitotic, polytene, and meiotic chromosomes of *Drosophila ananassae*. J. Hered. *66*, 353-361.

HSU, T.C. (1949): The external genital apparatus of male Drosophilidae in relation to systematics. Univ. Texas Publ. *4929*, 60-142.

KANESHIRO, K. and M.R. WHEELER (1970): Preliminary report on the species *Drosophila ananassae* subgroup. Dros. Inf. Serv. *45*, 143.

KOPP, A. and J.R. TRUE (2002): Phylogeny of the Oriental drosophila melanogaster species group: a multilocus reconstruction. Syst. Biol. *51*, 786-805.

KOPP, A. and O. BARMINA (2005): Evolutionary history of the *Drosophila bipectinata* species complex. Genet. Res. *85*, 23-46.

LEMEUNIER, F., S. AULARD, M. ARIENTI, J.M. JALLON, M.L. CARIOU, L. TSACAS (1997): The *ercepeae* complex: new cases of insular speciation within the *Drosophila ananassae* species subgroup (*melanogaster group)* and description of two new species (Diptera: Drosophilidae). Ann. Entomol. Soc. Am. *90*, 28-42.

LEMEUNIER, F., L. TSACAS, J.R. DAVID, M. ASHBURNER (1986): The melanogaster species group. In Thompson, J. R. Carson, H.L. (Editors). The genetics and biology of *Drosophila*, Vol 3e Academic Press, New York, Pp 147-256.

MATSUDA, M., C.S. NG, M. DOI, A. KOPP, Y.N. TOBARI (2009): Evolution in the *Drosophila ananassae* species subgroup. Fly *3*, 157-169.

MATSUDA, M. and Y.N. TOBARI (1999): A parthenogenetic strain of *D. pallidosa*-like in the *D. ananassae* complex. Dros. Inf. Serv. *82*, 49-50.

MATSUDA, M. and Y.N. TOBARI (2004): Genetic analysis of several *Drosophila ananassae* complex species show a low frequency major gene for parthenogenesis that map to chromosome 2. Genet. Res. *83***,** 83-39.

MAYR, E. (1963): Animal Species and Evolution. Belknap, Harvard.

MC EVEY, S.F., J.R. DAVID, L. TSACAS (1987): The *Drosophila ananassae* complex with description of a new species from French Polynesia (Diptera: Drosophilidae). Ann. Soc. Entomol. Fr. *23*, 377-385.

MORIWAKI, D., Y.N. TOBARI (1993): Catalog of mutants. In Tobari, Y.N. (Editor) *Drosophila ananassae*: genetical and biological aspects. Japan Scientific Society Press, Tokyo, Pp.209-259.

NANDA, P. and B.N. SINGH (2011a): Effect of chromosome arrangements on mate recognition system leading to behavioural isolation in *Drosophila ananassae*. Genetica *139*, 273-279.

NANDA, P. and B.N. SINGH (2011b): Origin of sexual isolation in *Drosophila ananassae* due to founder effects. Genetica *139*, 779-787.

NEMOTO, T., M. DOI, K. OSHIO, M. MATSUBAYASI, Y. OGUMA, T. SUZUKI, Y. KUWEAHARA (1994): (Z,Z)-5, 27 tritracontadient: major sex pheromone of *Drosophila pallidosa* (Diptera : Drosophilidae).J. Chem. Ecol. *20*, 3029-3037.

POLLARD, D.A., V.N. IYER, A.M. MOSES, M.B. EISEN (2006): Widespread discordance of gene trees with species tree in *Drosophila*: evidence for incomplete lineage sorting. Plos Genet. *2*, 173.

ROY, V., L. MONTI-DEDIEU, N. CHAMINADE, S. SILJACK YAKOVLEV, S. AULARD, F. LEMEUNIER, C. MONTCHAMP-MOREAU (2005): Evolution of the chromosomal location of rDNA genes in two *Drosophila* species subgroup: *ananassae* and *melanogaster*. Heredity *94***,** 388-395.

SAWAMURA, K., Y. TOMIMURA, H. SATO, H. YAMADA, M. MATSUDA, Y. OGUMA (2006): Establishing interspecific mosaic lines between *Drosophila ananassae* and *D. pallidosa* by means of parthenogenesis. Genet. Res. *88*, 1-11.

SAWAMURA, K., H. ZHI, K. SETOGUCHI, H. YAMADA, T. MIYO, M. MATSUDA, Y. OGUMA (2008a): Genetic analysis of female mating recognition between *Drosophila ananassae* and *Drosophila pallidosa*: application of interspecific mosaic genome lines. Genetica *133*, 179-185.

SAWAMURA ,K., K. KOGANEBUCHI, H. SATO, K. KAMIYA, M. MATSUDA, Y. OGUMA (2008b): Potential gene flow in natural populations of the *Drosophila ananassae* species cluster inferred from a nuclear mitochondrial pseudogene. Mol. Phylogenet. Evol. *48*, 1087-1093.

SAWAMURA, K., K. KAMIYA, H. SATO, Y. TOMIMURA, M. MATSUDA, Y. OGUMA (2010): Evolutionary relationship in the *Drosophila ananassae* species cluster based on introns of multiple nuclear loci. Zool. Sci. *27*, 303-312.

SCHAWAROCH, V. (2002): Phylogeny of a paradigm lineage: the *Drosophila melanogaster* lineage group (Diptera: Drosophilidae). Biol. J. Linn. Soc. *76*, 21-37.

SCHUG, M.D., E.E. REGULSKI, A. PEARCE, S.G. SMITH (2004): Isolation and characterization of dinucleotide repeat microsatellites in *Drosophila ananassae* Genet. Res. *83*, 19-29.

SCHUG, M.D., S.G. SMITH, A. TOZIER-PEARCE, S.F. MC EVEY (2007): The genetic structure of *Drosophila ananassae* populations from Asia, Australia and Samoa. Genetics *175*, 1429-1440.

SCHUG, M.D., J.F. BAINES, A. KILON-ATWOOD, S. MOHANTY, A. DAS, S. Z. GRATH, S.G. SMITH, S. ZARGHAM, S.F. MC EVEY, W. STEPHAN (2008): Evolution of mating isolation between populations of *Drosophila ananassae* Mol. Ecol. *17*, 2706-2721.

SINGH, B.N. (2000): *Drosophila ananassae*: a species characterized by several unusual genetic features. Curr. Sci .*78*, 391-398.

SINGH, B.N. (2010): *Drosophila ananassae* : A good model species for genetical, behavioural and evolutionary studies. Ind .J. Exp. Biol. *48*, 333-345.

SINGH, P. and B.N. SINGH (2007): Population genetics of *Drosophila ananassae*: genetic differentiation among Indian natural populations at the level of inversion polymorphism. Genet. Res. *89*, 191-199.

SINGH, P. and B.N. SINGH (2008): Population genetics of *Drosophila ananassae.* Genet. Res. *90*, 409-410.

SISODIA, S. and B. N. SINGH (2010a): Influence of developmental temperature on cold shock and chill-coma recovery in *Drosophila ananassae:* acclimation and latitudinal variations among Indian populations. J. Therm. Biol. *35*, 117-124.

SISODIA, S. and B. N. SINGH (2010b): Resistance to environmental stress in *Drosophila ananassae:* latitudinal variation and adaptation among populations. J. Evol. Biol. *23*, 1979-1988.

SPIETH, H.T. (1966): Mating behaviour of *Drosophila ananassae* and *ananassae* like flies from the Pacific. Univ. Texas Publ. *6615*, 133-145.

STALKAR, H.D. (1951): Diploid parthenogenesis in the *cardini* species group of *Drosophila.* Genetics 36, 577

STALKAR, H.D. (1954): Parthenogenesis in *Drosophila.* Genetics *39*, 4-34.

STONE, W.S., M.R. WHEELER, F.D. WILSON, V.L. GERSTENBERG, H. YANG (1966): Genetic studies of natural populations of *Drosophila* II. Pacific Islands Populations. Univ. Texas Publ. *6615*, 1-36.

THROCKMORTON, I.H. (1975): The phylogeny, ecology and geography of *Drosophila*. In: King, R. (Editor). The Handbook of *Drosophila*. Vol. 3, Plenum New York, Pp 421-469.

TOBARI, Y.N. (1993): *Drosophila ananassae*: Genetical and Biological Aspects. Japan Scientific Society Press, Tokyo.

TODA, M.J. (1991): Drosophilidae (Diptera) in Myanmar (BURMA) VII. The *Drosophila melanogaster* species group, excepting the *D. montium* species group. Orient Insects *25*, 69-94.

TOMIMURA, Y., M. MATSUDA, Y.N. TOBARI (1993). Polytene chromosome variation in *Drosophila ananassae* and its relatives. In Tobari, Y.N. (Editor) *Drosophila ananassae*: Genetical and Biological Aspects. Japan Scientific Society Press, Tokyo, Pp. 139-151.

TSACAS, L. (1984): Nouvelles donnees sur la biogeographie et l'evolution du groupe *Drosophila melanogaster* en Afrique. Description de nouvelles especes (Diptera: Drosophilidae). Ann. Soc. Entomol. Fr. *20*, 419-438.

VISHALAKSHI, C. and B.N. SINGH (2006): Sexual isolation between two sibling species of *Drosophila*: *D. ananassae* and *D. pallidosa*. Curr. Sci. *90*, 1003-1006.

WONG, A., J. D. JENSEN, J.E. POOL, C.F. AQUADRO (2007): Phylogenetic incongruence in the *Drosophila melanogaster* species group. Mol. Phylogenet. Evol. *43*, 1138-1150.

YAMADA, H., M. MATSUDA, Y. OGUMA (2002a): Genetics of sexual isolation on courtship song between two sympatric species: *Drosophila ananassae* and *D. pallidosa.* Genetics *116*, 225-237.

YAMADA, H., T. SAKAI, M. TOMARU, M. DOI, M. MATSUDA Y. OGUMA (2002b): Search for species specific mating signal in courtship songs of sympatric sibling species *Drosophila ananassae* and *D. pallidosa*. Genes Genet. Syst. *77*, 97-106.

YAMADA, H., M. TOMARU, M. MATSUDA, Y. OGUMA (2008): Behavioural sequence leading to sexual isolation between *Drosophila ananassae* and *D. pallidosa*. J Insect. Behav. *21*, 221-219.

ZHANG, Y., D. STURGILL, M. PARISI, S. KUMAR, B. OLIVER (2007): Constraint and turnover in sex-biased gene expression in the genus *Drosophila*. Nature *450*, 233-237.

KOMPLEKS *Drosophila ananassae* VRSTE: EVOLUCIONI ODNOS MEĐU RAZLIČITIM ČLANOVIMA

B.N. SINGH i Seema SISODIA

Genetička laboratorija, Odelenje zoologije, Banaras Hindu Univerzitet,
Varanasi-221 005, INDIA,

Izvod

Informacija o genetičkoj strukturi i istorijskoj demografiji prirodnih populacija je ključna u razumevanju načina uticaja prirodne selekcije na promene genoma. *Drosophila ananassae* je široko rasprostranjena vrsta koja se nalazi u geografski izolovanim ili delimično izolovanim populacijama i pretstavlja jedinstvenu mogućnost za ispitivanja stukture populacije i molekularnog variranja. *D. ananassae* i bliske srodne vrste služe kao široko korišćen model u populacionoj i evolucionoj genetici. *Ananassae* podgrupa pripada *melanogaster* vrsti grupe. Ova podgrupa sadrži 22 opisane vrste raspoređene uglavnom u jugoistočnoj Aziji, sa nekim vrstama koje su se proširile u severoistočnu Australiju, Južni Pacifik I Indijski podkontinent i Afriku. Unutar *ananassae* podgrupe , kompleks tri vrste - *ananassae, bipectinata and ercepeae* se prepoznaju na osnovu morfologije muških genitalija. *D. ananassae* I njeni srodniic imaju mnoge prednosti kao model genetičke diferencijacije i specijacije. U radu su diskutovani distribucija, filogenija, hibridizacija i polna izolacija *D. ananassae* kompleksa vrsta. Kompleks nekoliko vrsta na izolovanim ostrvima obzbeđuju koistan model za evoluciona ispitivanja preko mehanizma specijacije.

Primljeno 21. VI. 2012.
Odobreno 08.IV. 2013.